ON TROPICAL TREE SEEDLINGS ${ }^{1}$<br>I. SEEDS, SEEDLINGS, SYSTEMS, AND SYSTEMATICS<br>by James A. Duke<br>Battelle Memorial Institute, Columbus Laboratories<br>Columbus, Ohio<br>Illustrated by Peggy K. Duke


#### Abstract

The scattered information on characters useful in seed and seedling identification is brought together and terms defined. The problem of information retrieval in identifying seedlings is discussed and an example given of the use of a polyclave for naming an unknown. Seedling characters are given for a number of tropical families.


## Introduction

For the past three years, as contractor to the Atomic Energy Commission, Battelle Memorial Institute, Columbus Laboratories, has been involved in a study of the biological feasibility of nuclear excavation of a sea-level canal in Panama or Colombia. Fiscal and temporal limitations forced emphasis on anthropological feasibility. My role, as botanist for the survey, has been to determine how man utilizes plants in the study area. Many times I have been faced with an isolated seed or fruit used by the natives. Other scientists, studying herbivore diets, may have only a seed from a fecal sample. Some of these can be identified, but usually only with difficulty. Internal morphology of the seeds provides valuable clues. Many of the seeds are still viable. Some exhibit improved germinability after passing through animals. Characters of the resulting seedlings offer more valuable clues. As seed coats often remain intimately associated with seedlings, it seems rather narrow-minded to divorce seed from seedling studies or vice versa. This introduction to the study of tropical tree seedlings presents some of the important terms and concepts.

## Seeds and Systematics

The importance of seeds to systematics is readily apparent in Gray's Manual (Fernald, 1950) where the second major division is termed "Spermatophyta" meaning seed-plants, but there are cultivated spermatophytes which bear no seeds. Subdivisions also bear titles reflecting seed characters, Gymnospermae and Angiospermae, depending on whether the carpels are open or closed, but there are exceptional angiosperms which have open carpels (Anchietea, Butomus, Decorsella, Firmiana, Mitrasacme, Moringa, Reseda, Trillium) (Melville, 1962). The classes, Dicotyledones and Monocotyledones, are based on the number of cotyledons but many dicots (especially in Caryophyllales and Ranales) have only one cotyledon normally developed. Some monocots, e.g., Arisaema, Arum, Commelina, Dioscorea, Paris, Rajania, Sagittaria, Tamus, Tinantia, Trichopus, and Trillium, regularly

[^0]Ann. Missouri Bot. Gard. 56(2): 125-161, 1969.
or aberrantly reveal traces of a second cotyledon. Some taxa are stenospermous with little seed variability, while others are euryspermous with much variability. Several Asteraceae and some Rubiaceae (with capitate inflorescences) have different types of seeds in the "ray" and "disc" flowers of the same capitulum. Species of Stellaria have capsules containing seeds with two types of sculpture, the percentages of each type being environmentally determined. In Axyris amaranthoides L., Martin (1946) reports two types of seeds from the same plant: (1) elliptic terminally alate, angular body, the surface flecked with small gray areas, (2) oval exalate, lenticular seeds with satiny dark gray body. Thus, seeds are important to systematics for the definitions of taxa, from the division to the subspecific categories.

Study of seeds will make one more sympathetic to segregation of the classic water lily assemblage into several families. Seeds of Ceratophyllum exhibit a rare combination of characteristics: (1) radicle not apparent, (2) plumule foliate, (3) testa spiniferous, (4) embryo investing, and (5) endosperm absent. The water lotus, Nelumbo, shares several fundamental characteristics with Ceratophyllum, such as (1) radicle not apparent, (2) plumule foliate, (3) embryo investing and endosperm absent [a correlated combination of characters rendering Martin's (1946) classification of the embryo as "broad" untenable]. An amateur readily could separate the seeds of Nelumbo and Ceratophyllum by their external morphology. Nymphaea, classically included in the same family with Nelumbo, has a radically different seed, which like its pollen, anatomy, etc., suggests monocotyledonous affinities. Definitive characters are (1) broad embryo, (2) puberulent lines, (3) white aril, and (4) copious amyloidiferous endosperm. Seed characters suggest that Nelumbo is closer to Ceratophyllum than to Nymphaea.

## Seeds and Retrieval Systems

Murley (1951) voiced the still-unfulfilled challenge "identification of isolated seeds is important in paleobotany, archaeology, and in the practical work of seed laboratories, for the seed is usually the only part of the plant available for identification. . . Seed keys should be great timesavers compared to the former trial and error process." A novice confronted for the first time with water lily seeds would probably need to spend hours or even days to find out to which family the seed belonged. Toward the solution of this novice's problems, Duke (1964a, b; 1965b, c, d, e) started the polyclave, an information-retrieval system designed primarily to facilitate identification of unknowns.

The polyclave is a coordinated index to around 800 characters, some rarely employed by seed technicians, e.g., latex, leaf type, germination type, indument, etc. Seed characters alone overcrowded the standard $5 \times 8$ edgepunch cards. The polyclave system recognizes 480 families arranged roughly after the Dalla Torre and Harms sequence. Abbreviations of these 480 families are shown in the Family Polyclave Underlay (Plate 1). Plate 1 also contains underlays for Missouri, Panama, and Viet Nam, with abbreviations of the families reported in their respective floras. These underlays, or positives, are printed in color, with plus signs in each corner. Plate 2 shows various character overlay cards or negatives updated
since publication of the polyclave. Negatives are printed in black and white or black and transparent and bear a minus (-) sign in each corner. Blanks in the overlays represent families recorded to have the characters. Acetate transparencies of these cards can be superimposed over the corresponding underlay or positive. Then only the abbreviations which show through in color correspond to families possessing the characters.

Seeds of the water lily allies afford good examples of the polyclave approach, but some poisonous fabaceous seeds afford a more colorful demonstration. In Plate 2, abbreviations of families reported to have red seeds have been erased. Superpose the corresponding transparency over the family underlay and you read in color abbreviations of those families reported to have red seeds. Similarly, superpose the transparency for black seeds over an underlay and you read in color only those families reported to have black seeds. Superpose both transparencies over the underlay and you read in color only those families reported to have both characters. Add to these the transparency for poisonous seeds, and you see in color only the few families reported to have the three characters. Refer to Figure 23 and note that the seedlings of Ormosia have stipels, a rare character reported only in those families whose abbreviations have been removed from the transparency for stipellate eophylls. Superpose all four transparencies and you will read in color "FAB," for Fabaceae, to which Ormosia belongs. With four transparencies, most families have been eliminated from consideration. In the polyclave (Duke 1969b) there are 770 character negatives scored for various taxonomic characters, about half of which are useful in determining the family of unknown seeds and seedlings. Superposition of any combination of these eliminates families not reported to have the characters. Theoretically, if an unknown has nine uncorrelated characters, each of which occurs in only half of the 480 families, superposition of the nine corresponding character transparencies would eliminate all but one family. Because of parallel evolution and flaws in existing classifications, however, several families may turn up, although perhaps few or no species in each may have the combination of nine characters. A retrieval system at the generic level would be more efficient, but it would be a sizeable chore to score some 20,000 genera, many with over a hundred species each, for a thousand characters. Beginnings have been made for the genera of grasses (Duke, Gunn, and Terrell, unpublished), legumes (Duke, 1965e, 1969), and palms (Duke, 1965d).

## Seeds

ovules Seeds, like other plant entities, defy rigid definition, but a common definition is "fertilized ovule." The angiosperm ovule consists of a central body, enclosed more or less completely by one or two integuments and supported on a basal stalk, the funicle. The central body consists of the nucellus, a distal part, in which sporogenous tissue is borne, and the chalaza, a basal part where funicle, integuments, and nucellus merge. In sessile ovules, the funicle is absent, but in some the funicle may be elongate and adnate to the ovule body forming a ridge, the raphe. The scar on mature seeds known as the hilum represents the point of attachment of the funicle (or carpel wall in sessile ovules). Generally there are one or two integu-








## AMILY POLYCLAVE
























































SEEDS BLACK









































```
Plate 2. Overlays from the family polyclave.
```



















ments, more or less fused to each other and to the central body, but in specialized ategmic types the integuments are absent, e.g., some Balanophorales and Santalales. The opening between the tips of the integuments where the nucellus is exposed is termed the micropyle. Arils, loosely defined as investing outgrowths from the chalazal region, have been questionably interpreted as third integuments and as primitive. Freedom of the nucellus from the integuments as in Amphipterygium, Cananga, Casuarina, Cleome, Juglans, and Myrica seems rare. Freedom of the two integuments occurs in some Amentiferae, Capparaceae, Fabaceae, Ranunculaceae, and Rosaceae. Where there are two, the outer usually is more massive and longer than the inner. Occasionally in the Annonaceae, Cactaceae, Proteaceae, and Trapaceae, the inner projects beyond the outer. Bitegmic anatropous ovules usually have only one integument obvious on the side adjacent to the funicle. Number of integuments is not a constant indicator of relationships. Most species of Populus have two integuments, but two species and all Salix species known, have only one (Eames, 1961). Peperomia has one integument, while other Piperaceae have two. Both integuments are absent in some Olacaceae and Opiliaceae. As a rule, gamopetalous dicots are unitegmic but Primulaceae and Cucurbitaceae are bitegmic.
ovular types Ovules are termed crassinucellar when the nucellus is massive and the megaspore mother cells are deep in the distal tissue and tenuinucellar when the nucellus is small and delicate and the spore mother cells (usually one) are directly below the epidermis. The two types intergrade. Crassinucellar is more primitive, usually accompanied by two integuments. The ovule is orthotropous (loosely synonymous with atropous) when straight and upright on the placental surface, with the micropyle distal and the funicle short or absent. It is anatropous when bent upon itself and more or less adnate to the funicle, with the micropyle facing the placenta. Cronquist (1968) states that the anatropous condition is eventually derived from the orthotropous. It is campylotropous when the ovule is reniform, attached near the middle, and the micropyle faces the placenta. It is amphitropous when the funicle is adnate to the ovule for about half its length and the micropyle faces laterally. Anatropy is more common and characterizes many primitive taxa (e.g., in Ranales, Helobiae, Nymphaeaceae). Orthotropy occurs in more specialized groups with solitary ovules and basal placentation Juglandaceae, Najadaceae, Piperaceae, Polygonaceae, and Restionaceae. Campylotropy characterizes Apocynaceae, Capparaceae, Caryophyllaceae, Geraniaceae, and Verbenaceae. Orthotropy, though superficially more simple, seems to be derived as in the Urticales. Ulmaceae and Moraceae have suspended anatropous ovules, Laportea is transitional and Urtica and Boehmeria have basal orthotropous ovules. Circinotropous or coiled ovules are rare but occur in Cactaceae.
stomatal types The outer integument has normal stomata (Eames, 1961), and in some cases, stomatal types may serve as indicators:

Actinocytic: Stoma encircled by a rosette of subsidiary cells.
Anisocytic ("cruciferous"): Stoma surrounded by three cells of which one is distinctly smaller than the other two.

Anomocytic ("ranunculaceous"): Stoma surrounded by a limited number of cells that are indistinguishable in size, shape, or form from those of the remainder of the epidermis. (Type 4; Stebbins and Khush, 1961.)

Diacytic ("caryophyllaceous"): Stoma enclosed by a pair of subsidiary cells whose common wall is at right angles to the guard cells.

Didymocytic ("arecaceous"): Stoma enclosed by four subsidiary cells, the pairs dissimilar. (Type 2; Stebbins and Khush, 1961.)
"Gramineous": Guard cells with the middle portions much narrower than the ends giving a dumbbell appearance in surface view. Stomata tend to disappear as the seed matures, but they are reported in Canna indica, Carpolyza spiralis, and Nerine bowdeni (Boyd, 1932).

Paracytic ("rubiaceous"): Stoma accompanied on either side by one or more subsidiary cells parallel to the long axis of the pore and guard cells. (Types 1 and 3; Stebbins and Khush, 1961.)

Triacytic ("gordoniaceous"): Guard cells with three subsidiaries similar to each other, but differentiated from the epidermis.
endosperm The so-called double fertilization results in two chains of events, the one leading to embryo formation, the other to endosperm formation. In all monocots and dicots so far investigated (Swamy and Ganapathy, 1957) endosperm formation follows one of three sequences in development.

Nuclear: Initial division and usually subsequent ones are not followed by wall deposition. Nuclei may remain free or later be separated by walls.

Cellular: First and several subsequent divisions accompanied by wall formation.

Helobial: A transverse wall is laid down following the initial division, dividing the embryo sac into a micropylar and a chalazal chamber. Subsequent divisions are generally free-nuclear and may take place in both chambers, but invariably the main bulk of the endosperm is formed by the micropylar chamber.

These developmental types will be of little use in identification of unknowns, but may be correlated with other characteristics. Sporne (1954), working on external morphological correlates concluded that the nuclear type was primitive, while Swamy and Ganapathy (1957), correlating with wood anatomy, concluded that the cellular type was less advanced. Cronquist (1968) notes that in the Gentianaceae, characterized by nuclear endosperm, two advanced mycotrophs, Voyria and Voryriella, have cellular endosperm. Presence or absence of endosperm is a useful character. Ruminations in the endosperm are frequently diagnostic, and may arise (1) through expansion of the developing endosperm into furrows in the integument or (2) through invagination into the endosperm of peripheral tissues. The latter may explain the peculiar tendency to cryptocotylar germination in some Annonaceae.

The chemical and physical nature of the endosperm is occasionally diagnostic. Dissection in water of many seeds characterized by oily endosperm will yield an
obvious oil-slick. The IKI starch test can be used to detect amyloidiferous endosperm in embryos. Simmondsia chinensis is unique among plants in that its seed oil is not a fat but a liquid wax.

Endosperm may be absorbed by the embryo before (exalbuminous seeds) or after germination (albuminous seeds). Cronquist (1968) notes that the absorption may take place rather late in ontogeny, as in many of the Sapotaceae, in which the endosperm is obvious in young seeds but wanting or scanty in mature seeds. In some germinating seeds, the endosperm is raised characteristically above the ground with or without the testa. In members of the Myrtales and many aquatics, the hypocotyl is the storage region, greatly swollen at the expense of the cotyledons to form the type of embryo termed macropodial. Perisperm, nutritive tissue derived from the nucellus or integuments, may be present in addition to endosperm, and is associated with the "peripheral" embryos of Martin (1946). Cronquist (1968) states that perisperm is clearly an advanced condition. During germination, the food is absorbed from the perisperm by the endosperm and thence is passed on to the embryo.
seed size and shape As Eames (1961) notes, both large and small seeds have been considered primitive. Large seed size has quite naturally been correlated with the tree habit, and therefore deemed primitive. For examples of variation in the families, witness the palms, with huge seeds like Cocos and small ones like Prestoea, and the legumes, with small seeds like Trifolium and large seeds like Mora. Nonetheless, the novice faced with an unknown could eliminate much work if he knew what groups had the same size seeds as the unknown.

The same is true of seed shapes. Who knows which shapes are most frequent - ellipsoid, reniform, lenticular, globose, ovoid, oblong, or segmentoid? Among the myriad of other shapes possible, some are quite rare, and the knowledge of which families exhibit which types can save an immense amount of random searching.
testa As the seed develops from the fertilized ovule, the integuments develop the seed coat or testa. Both integuments may still be recognizable in some Euphorbiaceae, Rosaceae, and Rutaceae, but more commonly the inner is lost or drastically reduced. In others, such as Opiliaceae and Pelliceriaceae, there is no testa. Appendages are quite often useful clues to affinities. Most important are wings, arils [fleshy transformations of the outer layers of the outer integument (= sarcotestae), of the chalaza or of the distal part of the funicle], arilloids (those developing from the micropylar rim of the integuments), strophioles (fleshy tissues restricted to crests, as along the raphe), caruncles (restricted to the base or apex of the seed), glochidiae, spines, tubercles, and various types of hairs, which may be more or less restricted to the dorsal surface of the seeds as in some Bombacaceae, Malvaceae, Convolvulaceae, and Caryophyllaceae or concentrated in comas at one end of the seed, as in some Onagraceae, Apocynaceae, and Asclepiadaceae. Specialized appendages, much resembling modifications of the caruncle, are cap-like operculi (e.g., in Commelinaceae) which seem to facilitate
emergence of the seedling, and coronae (apical annular crowns as occur in certain Boraginaceae and Euphorbiaceae). Several seeds exhibit combinations of the above characteristics, and several of the above characteristics intergrade. Corner (1954) suggests that the truly arillate seed is primitive in angiosperms, but arils and sarcotestae are generally regarded as adaptations for seed dispersal. Alate and comose seeds are clearly derived adaptations when compared to seeds with no special dispersal mechanisms.

Less prominent markings of the testa have been treated in detail by Murley (1951), and an elaborate terminology has been erected and illustrated. Brown probably is the most frequent seed color, with other colors occurring in less than half the families. Particular types of seeds, often seen in necklaces, are ocellate and halonate seeds, which are frequent in legumes. Ocellate seeds have a large spot of color, like an eyeball, such as the black-eyed red seeds of Abrus, Ormosia, etc. Halonate seeds have a circle of lighter or darker color prominent in the seed as in Enterolobium cyclocarpum (Duke, 1965a).
chemistry Earle and Jones (1962) published results of chemical analyses of seed samples from 113 plant families and their research continues to expand the number of families, genera, and species investigated. Valuable biochemical data presented at a specific level are percent ash, protein, and oil; weight per 1000 seeds; fraction of alcohol-soluble nitrogen; fraction of trichloracetic-acid-soluble nitrogen, reactions of starch test, alkaloid test, tannin test, etc.
utility and geography Most botanists at several points in their career will have received seeds for identification with no other information than: "This seed is used by the natives (1) to poison fish, (2) to eat raw, (3) to make necklaces, (4) to poison animals, (5) as an anthelmintic, (6) as an oil source, (7) pulverized as an insecticide, (8) as a starch source, (9) as a candle, etc." Or the letter may read, "The enclosed seed was found: (1) germinating in sea drift, (2) among the belongings of a jazz musician, (3) to constitute $90 \%$ of the tufted titmouse's food intake, (4) clinging to the clothing of an exile Cuban, (5) in a Navajo campsite, (6) mixed in with pollen 1000 feet above New York City, (7) to cause dermatitis among three prisoners, (8) in the ejecta of a regurgitating child, (9) as a frequent fossil in a Pleistocene deposit, etc."

Unsolicited letters arrive by the hundreds in botanical gardens all over the world with statements like the above followed by the question "What is it?" Responsible taxonomists faced with such queries have spent days combing the literature to find out which seeds are barbascos, poisonous, edible, common in sea drift, airborne, allergenic, ornamental, etc. It is sad that most of their handscribbled notes could not be transcribed to an information retrieval system available to subsequent botanists.

Knowledge of the origin of the seed can be equally useful if entered into the system. There are many genera with brilliant red seeds, but how many occur in your backyard, in your state, in your country, in your continent, in your hemisphere?

## Embryo

proembryo The following key serves to distinguish the main types of proembryo:
I. Division of zygote longitudinal. . . . . . . . . . . . . . . . . . . . . . . Piperad type
II. Division of zygote transverse:
A. Division in terminal cell transverse:

1. Basal cell plays essential part in development
of the embryo proper . . . . . . . . . . . . . . . Chenopodiad type
2. Basal cell plays no essential part in development of the embryo proper:
(a) Basal cell divides no further and becomes a large suspensor cell (suspensors of a few cells, but derived from the terminal cell, may be present)

Caryophyllad type
(b) Basal cell usually forms a suspensor of two or more cells

Solanad type
B. Division in terminal cell longitudinal:

1. Both basal and terminal cells take part in further development of embryo .Asterad type
2. Basal cell plays little or no part in development of the embryo Onagrad type
("crucifer type") Further information on embryology will be found in Davis (1966).
embryo Martin (1946) recognized 12 embryo types among seed plants. Some categories overlap with others, but this in no way destroys their taxonomic usefulness. Some of his categories are broad and are subdivided in the polyclave.
A. Basal (Embryo at One Pole of Seed)
3. Rudimentary: Small, nonperipheral embryo in medium to large seed, more than 2 mm long, the endosperm copious but rarely starchy. Martin has taken this type as the progenitor of the other types in a novel phylogenetic scheme based on embryo types. It roughly groups the Centrospermae on a limb equivalent to the monocot and dicot limbs. Large seeds with small embryo and copious endosperm are rather characteristic of both the woody and herbaceous Ranales and are frequent in the LiliaceaeAmaryllidaceae alliance as well as in palms and sedges. Intergrading with the rudimentary are two small categories, the Broad and the Capitate.
4. Broad: A globular or lenticular embryo in copious starchy endosperm. Martin lists few examples of the broad embryo. Nelumbonaceae, which has anything but a broad embryo as defined by Martin, should be classified as investing. Broad embryos occur infrequently in aquatic or palustrine, more or less primitive dicots and monocots, and in a few parasites.
5. Capitate: A capitate or turbinate, more or less basal, embryo in copious starchy endosperm. Closely related to the broad embryo, this type occurs in about ten families. Capitate and broad embryos seem to be correlated with operculate seeds.
6. Lateral: Although characteristic of more genera than the preceding, the lateral embryo is characteristic of fewer families, one of them being the grasses. Reeder (1957) illustrates the usefulness of the embryo in grass systematics. Embryos of Cynomoriaceae, Bromeliaceae, and Centrolepidaceae could be included according to the definition "embryo basal-lateral or lateral and evident from the exterior, usually with copious starchy endosperm." The lateral subdivision, found only in monocots, except for apparent occurrence in Cynomoriaceae, indicates a transition to the Peripheral division.

## B. Peripheral

Embryo ordinarily elongate and large, quarter to dominant, contiguous in part, at least to the testa; perisperm starchy, central or rarely lateral; cotyledons narrow or expanded; dicots with one cotyledon occasionally abortive. This roughly coincides with the Centrospermae but other taxa approach the peripheral condition, e.g., members of Cactaceae, Cuscutaceae, Frankeniaceae, Ulmaceae, etc. (To further suggest the resemblance of Centrospermae to monocots, consider also the farinose starchy endosperm, characteristic of the Farinosae of monocots, and the tendency toward geniculate, ensheathed nodes.) In the peripheral division are straight, arcuate, hippocrepiform, annular, and spirolobal embryos. Many dicot peripheral embryos have the second cotyledon reduced (anisocotylar, as in Wittia, Fig. 60) or absent. Peculiarities shared by many families with peripheral embryos are possession of beta-cyanin and polyporate pollen grains. Polyporate pollen grains also occur in Alismataceae where, e.g., Sagittaria has rudiments of a second cotyledon.
C. Axile

1. Linear Subdivision:
(a) Linear: Embryo axial, generally several times longer than broad, straight, curved or coiled; cotyledons not expanded; seeds normally not minute; endosperm not starchy (rarely so in monocots). Martin notes a distinct group, Cannaceae, Marantaceae, Pontederiaceae, Sparganiaceae, and Zosteraceae, which are unique among linear seeds in having starchy endosperm and in having the base of the embryo extend into a depression at one end of the seed, as in some Commelinaceae, and Arecaceae, in Caulophyllum thalictroides (Podophyllaceae), and perhaps in Loranthaceae. The linear division is well represented in gymnosperms, monocots, and dicots. Included are straight, arcuate, hippocrepiform, annular, and spirolobal embryos with or without endosperm. These could be separated from their peripheral counterparts only by the excentric endosperm which
supposedly would not give a starch test when present. Many aquatic monocots absorb all the reserves into a "foot." Macropodial embryos occur, e.g., in Alismataceae, Clusiaceae, Hydrocharitaceae, Lecythidaceae, Welwitschiaceae, Zosteraceae, etc.
(b) Dwarf: Embryo variable in relative size, small to total, generally stocky, cotyledons often poorly developed; seeds exclusive of testa mostly $0.3-2.0 \mathrm{~mm}$ long, often nearly as broad as long. This type occurs in many sympetalous families, e.g., Ericaceae, Gentianaceae, Loganiaceae, Scrophulariaceae, and Solanaceae. Parasitic derivatives of these are more likely to have the following:
(c) Micro: Seeds usually minute, less than 0.2 mm long, exclusive of testa, few-celled ( 50 to 150) ; embryo undifferentiated to total.
2. Foliate Subdivision:
(a) Spatulate: Embryo erect; cotyledons variable, thin to thick and slightly expanded to broad. The spatulate type occurs in more families than any other, closely rivaled by the linear (Martin, 1946). Since these are most common, they are least valuable for purposes of identifying unknowns. It would be practical to divide the spatulate into subclasses based on cotyledon shape and relative lengths of hypocotyl and cotyledon (the $\mathrm{H}: \mathrm{C}$ ratio in the polyclave).
(b) Bent: With expanded cotyledons in an axile position but with the cotyledons bent upon the hypocotyl in a jackknife fashion; cotyledons are generally thick or planoconvex but not necessarily so. In the commonest type, the bend is in the plane of the cotyledons, i.e., accumbent (pleurorhizal) $(0=)$. The bend may be contra the cotyledonary plane, i.e., incumbent (notorhizal) (o \| ) . The oblique embryo is intermediate between accumbent and incumbent ( $0 / / /$ ). The term oblique is unfortunate since certain "linear" embryos are oriented obliquely to the long axis of the seed, e.g., Clintonia. In a fourth type (orthoplocal), the cotyledons in addition to being incumbent, are conduplicate ( $0 \gg$ ). Such an embryo occurs in Avicennia. Martin would probably have classified this as a "folded" embryo. Spirolobal embryos have incumbent cotyledons, once folded (o $\|\|)$ while diplecolobal embryos have two or more folds $(0\|\|\|)$. All these "bent" embryos occur within the Brassicaceae and sporadically in other families. Rare convolute cotyledons occur in Terminalia.
(c) Folded: "Embryo with cotyledons usually thin, extensively expanded and folded in various ways." Many of the embryos diagrammed by Martin could be called incumbent or diplecolobal. Weirdly folded or contortuplicate cotyledons are frequent in the Sapindales and Malvales. The Convolvulaceae, also characterized by folded cotyledons, frequently share with the Malvaceae and Myrtaceae the characteristic of punctate cotyledons.
(d) Investing: The last of Martin's categories is defined under his AXILE division: "Embryo erect and with thick cotyledons overlapping and encasing the somewhat dwarfed stalk for at least half its length; endosperm wanting or limited." This would merge at the halfway point with both the folded and the spatulate types. Species having both foliate plumules and straight embryos would usually fit this category. Investing embryos are not common, but frequently are associated with cryptocotylar germination.

## Polyembryony

Polyembryony, the presence of more than one embryo in an ovule or seed, is not uncommon, and is characteristic of some groups. Secondary embryos may be adventive, arising from mother sporophytic tissue, or may derive from cleavage of the daughter sporophyte (embryo), or they may be haploid and derived from gametophytic nuclei other than the egg. Adventive embryos of nucellar origin are more common than those of integumentary origin, and have been said to exist in 19 percent of Trillium undulatum ovules. Citrus, Eugenia, and Mangifera are tropical genera notorious for polyembryony.

## Dormancy and Vivipary

Some seed technologists avoid the use of internal morphology and the seedling. Many small seeds germinate rapidly without scarification and the seedling yields additional characters for determination of an unknown. Faced with seeds brought to me for identification in Panama, I planted the seeds and ten days later had seedlings of Cannabis (Fig. 10), thereby confirming my suspicions. Some seeds are germinating before they are shed. In Cycadaceae and Ginkgoaceae, there may be no embryo when the "seed" is shed, but in most if not all angiosperms, the embryo is present in some stage of development, frequently continuing its development after shedding. Some seem to have no dormant period, e.g., Annona, Durio, Myristica, and Thalassia. Eames (1961) suggests that dormancy represents an advanced stage in the evolution of the seed. After-ripening-morphological and physiological-may delay readiness to germinate until long after shedding. Eames states that size of seed seems less important, from the standpoint of primitiveness, than time of inception of dormancy and stage of specialization of the embryo. Since primitive gymnosperms and a few angiosperms lack dormancy, and since there is a long-continuing, after-ripening process in some primitive families, absence of dormancy seems primitive. Duke (in press) finds larger seeds and quicker germination in species of the rain forest than in drier forest types.

Examples reported by Eames (1961) of time necessary to complete growth from seed-shedding stage to germinating stage are Fumaria, 8 days; Caltha, 10 days; Clematis, 17 days; Actaea, Hepatica, and Thalictrum, 2 months; Cocos, Fraxinus, and Paris, 4 months; Crocus, 6 months; Corydalis, 10 months; Trillium, 12 months. Data presented by Marrero (1949) for tropical tree species, suggest that cryptocotylar species (22) average 41 days between sowing and germination while phanerocotylar species (35) average 23 days.

Vivipary, an obvious example of lack of dormancy, has been attributed to some tropical tree species, especially mangroves. Seeds not truly viviparous, e.g., Capparis, Hura, and Inga (Fig. 17), have been reported as germinating before falling from the tree, but such cases are probably due to unusual meteorological conditions rather than inherent characteristics of the species. Often, seedlings will be found intimately associated with fruits on the forest floor. On account of such an association, the author was able to identify the seedlings of Apeiba, Clusia, and Enallagma, all with many-seeded fruits, sometimes important in mammal diets. The flattened subspherical tuberculate fruits of Apeiba, the 5-locular superior fruits of Clusia, and the large globose fruits of Enallagma offer combinations of characters occurring in few families. The combination of operculate fruits with palmilobed cotyledons that characterizes Cariniana (Fig. 66) apparently occurs only in the Lecythidaceae. Coupling fruit characters with those of the seeds and seedlings renders determinations more certain.

A second dormancy occurs in many tropical seedlings, in the dipterocarps in Asia and, e.g., in Connarus (Fig. 16) and Ormosia (Fig. 23) in Panama. Such species go into a state of dormancy after the cotyledons and first eophylls are raised and fully expanded, awaiting some ecological trigger to further their development.

## SEEdLings

germination There are two types of germination, phanerocotylar, in which the cotyledons emerge from the seed, and cryptocotylar, in which the cotyledons do not emerge from the seed (Duke, 1965a). Phanerocotyly is more common in dicotyledons, cryptocotyly in monocots. The peanut is a transitional type, while many genera have species with both types, e.g., Acer, Bauhinia, Caesalpinia, Clematis, Couratari, Lecythis, Ormosia, Passiflora, Phaseolus, Pithecellobium, Prunus, Pterocarpus, Quercus, Rhamnus, Rubia, Sapindus, Sophora, Sterculia, Terminalia, Theobroma, and Trichosanthes. Eames (1961) states that the hypogeal (cryptocotylar) method is clearly advanced. However, in Phaseolus, cryptocotyly is a Mendelian dominant to phanerocotyly (Compton, 1912). Among cryptocotylar dicots, two types seem rather rare and definitive: those in which scale leaves (cataphylls) preceding the foliage leaves are opposite (Bignoniaceae, Clusiaceae, Melastomaceae). The common type has small spiral or alternate cataphylls preceding the foliage leaves as in Gustavia (Fig. 65). Annonaceae, Hura, and several Rubiaceae, e.g., Pentagonia (Fig. 77) and Tocoyena (Fig. 79) exhibit a peculiar transitional condition. The cotyledons tardily emerge from the seeds, or may break off in the seed, unless man or accident breaks the seed coat. Usually the radicle is the first structure to emerge from the seed, but rarely the plumule emerges first.

The hypocotyl is the portion of the axis where the stem-root transition occurs. Occasionally there is an external demarcation, the collet, between hypocotyl and root. The cryptocotylar forms are often described as being devoid of hypocotyl, but the transition must occur. Compton (1912) has differentiated three types of transition in the legumes. The epicotyl, the embryonic axis above the cotyledonary
node, is often not obvious in the seed until after germination, but it tends to be better developed in cryptocotylar species before germination.
seedling axis After germination, the distinction between hypocotyl and epicotyl is more easily made (cf. Virola, Fig. 12). Frequently the hypocotyl will be swollen, pegged, or annulate near the soil. In many woody species such as Tamarindus and Virola (Fig. 12) the epicotyl and hypocotyl have different induments and textures. In species destined to become stilted or buttressed, such as Cecropia peltata and Sloanea berteriana, adventitious roots are often obvious at the seedling stage (Duke, 1965a). Swollen hypocotyls are not uncommon in species destined to have swollen trunks.

In Puerto Rican tree seedlings studies (Duke, 1965a), all laticiferous species except Pterocarpus had obvious latex by the first eophyll stage. In the seedling stage, Bursera and Dacryodes already exhibit the characteristic aroma of turpentine; seedlings of many Lauraceae and Myrtaceae, e.g., Pimenta, may be distinguished by their odors; seedlings of Cedrela odorata and Cordia alliodora are said to possess the characteristic alliaceous odor. A notebook containing a seedling of Quararibea smells about as pleasant as a herbarium case containing dried specimens. Spines may be evident quite early (second eophyll stage in Acacia farnesiana) (Duke, 1965a) and tardily develop in the axils of the cotyledons of Pereskia bleo.

Bailey's survey (1956) of 99 dicot families showed that 77 percent of the seedlings have an even number of strands at the cotyledonary node, and 60 percent of the cotyledons have two independent traces related to a single gap. The double-trace, unilacunar node is not confined to a few genera, but is of common occurrence in many orders of dicotyledons. This contrasts markedly with the foliar nodes, where the majority of dicots have an odd number of traces. The doubletrace unilacunar node has been reported for foliar nodes only in certain Amborellaceae, Austrobaileyaceae, Calycanthaceae, Chloranthaceae, Hernandiaceae, Lamiaceae, Lactoridaceae, Lauraceae, Solanaceae, Trimeniaceae, and Verbenaceae. Bailey observed no cotyledons with multilacunar attachments, but pentalacunar attachments are reported for Fitchia speciosa (Asteraceae) and multilacunar for Gustavia (Lecythidaceae) (Carlquist, 1961).

If the trilacunar condition is primitive, and ontogeny recapitulatory, one would expect ontogenetic reduction of trilacunar to unilacunar nodes. No seedling studied by Bailey displayed such reduction; on the contrary, first eophylls of a considerable number examined were unilacunar succeeded by tri- or even multilacunar nodes. Unilacunar nodes are usually associated with exstipulate leaves, while trilacunar and multilacunar are associated with stipules (Carlquist, 1961).

Two is the common number of traces in the lower taxa of both dicots and monocots, but four or three by fusion of the middle pair are frequent. Large numbers seem uncommon but occur in some Araceae and Cannaceae. In many monocots there are two strong lateral traces supplying the sides of the sheathing leaf base.

According to Eames (1961), the vascular cylinder of primary roots of seedlings is commonly diarch or tetrarch. Monarchy is rare in primary roots. Polyarchy
is frequent in monocotyledons. Tetrarchy has been considered more primitive than diarchy because of association with woody types, as for example in the Fabaceae. In Ranales, the Ranunculaceae have diarch while woody families have tetrarch primary roots. In Asteraceae both types occur, with neither obviously associated with primitive types. In dicots there are few variations from tetrarchy and diarchy, but in monocots, polyarchy with $4,6,8$, or 12 poles is not uncommon.
cotyledon number It has been suggested by Eames (1961) that dicotyly is the rule among angiosperms and gymnosperms, and that such features as polycotyly, schizocotyly, anisocotyly, gamocotyly, monocotyly, and cryptocotyly are derived. Pseudomonocotylar embryos may result from the conferruminate (gamocotylar) condition as in Eugenia, Nelumbo, Rhizophora, etc., or from reduction of one of the cotyledons, as in species of Abronia, Carum, Claytonia, Corydalis, Cyclamen, Dicentra, Eranthis, Erigenia, Mammillaria, Peperomia, Pinguicula, Ranunculus, Scaligera, Trapa, etc. Cronquist (1968) notes in Peperomia a gradual differentiation of two cotyledons for different functions: P. pellucida has two equal cotyledons which are withdrawn to become the first functional leaves of the seedling; P. peruviana also has two, but only one is withdrawn from the seed, the other remains to function as an absorbing organ; P. parvifolia has two initially unequal cotyledons - the larger remains within the seed coat as an absorbing organ, the smaller becoming the first leaf of the seedling, a situation hardly to be distinguished from that in many monocots. In some Gesneriacae, the cotyledons are the only leaves the plant develops. Among monocots, some Alismataceae, Araceae, Commelinaceae, and Dioscoreaceae show rudiments of a second cotyledon. Anisocotyly is well exemplified by such embryos as Petiveria.

Tricotyly is a frequent aberration, occurring in such diverse plants as coffee, maple, mesquite, and walnut. Polycotyly has been reported for 2 to 4 percent of the "British flora" (Eames, 1961), and is frequent in parasitic dicots, e.g., Loranthus, Nuytsia, and Persoonia. In woody Ranalean taxa, the percentage of tricotylar embryos may reach as high as 87 percent, with 13 percent tetracotylar and none dicotylar (Eames, 1961). In some cases, e.g., conifers and crucifers, the two cotyledons may be so deeply lobed as to appear tetracotylar. In Podocarpus coriaceus (Duke, 1965a), the first pair of leaves is attached so close to the cotyledonary node as to give the seedling a tetracotylar appearance. Superficially the cotyledons and eophylls appear similar but the cotyledons have two veins prominent while the eophylls have only one.

Lobing of the cotyledons appears to be constant in some taxa such as Bursera, Dacryodes, Lepidium, and Tilia where the lobing is palmate and in Amsinckia, Eschscholzia, Eucalyptus, Haematoxylum, Ipomoea, Pittosporum, Pterocarya, and Schizopetalon, where the cotyledons are deeply bifid. Retuse cotyledons are more or less characteristic of Bignoniaceae and Convolvulaceae. Lobed cotyledons are not necessarily correlated with lobed leaves. Peculiar combinations such as trifoliolate cotyledons and entire eophyll 1 (Bursera), entire cotyledons, and trifoliolate eophyll 1 (Ceiba), bilobate cotyledons and paripinnate eophyll 1 (Haema-
toxylum), retuse cotyledons and imparipinnate eophyll 1 (Jacaranda) can be very diagnostic.

Plicate, crenate cotyledons seem to be characteristic of the arboreal segregates of the Boraginaceae. Glandular margins occur on the cotyledons of several seedlings whose adult leaves also have glandular margins (Rosaceae, Rutaceae, etc.).

## Cotyledon

SHAPE AND SIZE Among entire cotyledons, there is a great variety of shapes and sizes which may be useful in determinations. Linear cotyledons are exceptional in some families, e.g., Dodonaea in Sapindaceae, and Spondias in Anacardiaceae, while they are the rule in others, especially in monocots and several dicots possessing "linear" embryos. Reniform cotyledons prevail in some families, especially those with "folded" and "spatulate" embryos (e.g., Bignoniaceae, Combretaceae, and Malvaceae). Many genera have species with narrow and species with broad cotyledons, e.g., Coreopsis and Galium.

Broad cotyledons are not necessarily followed by broad leaves. Coccoloba, Fagus, Gomidesia, Hakea, and Myrcia have species in which the cotyledons are broader than long while the eophylls are longer than broad. Other species have very narrow cotyledons followed by broad eophylls, e.g., Acer, Cissampelos, Cochlospermum, and Menispermum. Absolute size of the expanded cotyledons is probably less important than relative size.

Auriculate cotyledons occur (e.g., many Fabaceae and Meliaceae) while integrading cordate cotyledons seem less frequent (e.g., some Ranunculaceae). Peltate cotyledons occur but rarely (e.g., Peperomia), peltate eophylls being more frequent (e.g., Hernandiaceae, Menispermaceae, Piperaceae, and Tropaeolaceae).
cotyledon venation Bailey (1956) notes than many cotyledons are characterized by having a pseudo-palmate or palmate-parallel venation. Such cotyledons, scored plinerved in the polyclave, commonly have three or more conspicuous primary veins that extend outward from a locus at the base of the cotyledons, the laterals diverging and often reconverging parallel to the margins. Many such cotyledons show a transition from an even number (2) of vascular strands at the nodal level to an odd number ( 3 or 5) of primary veins in the lamina. There are numerous deviations from this common type, even among seedlings of the same genus or species. Cotyledons with different forms and venations may have similar basal (nodal) vasculatures and conversely cotyledons of similar form may have different nodal patterns.

Pinnate venation is less frequent in cotyledons than in foliage leaves, but there are more penninerved cotyledons among those attached at a single-trace node. Parallel venation is the common type in monocotyledons. In cryptocotylar forms, whose cotyledon tips are modified for suctorial purposes (scutellum), there is usually only one trace which divides to form a median and two strong lateral bundles, but only the median vein continues to the scutellum. In more primitive forms, in which there is little or no downbending of the distal part, all the vascular bundles, including those of the sides of the sheath, usually continue into the scutellum.

Carlquist (1961) notes that seedling anatomy is adduced as evidence of the origin of monocots from dicots but adds that vascular anatomy of cotyledons is perhaps of little significance because the duality of traces in each dicot cotyledon is as frequent as the well-known duality of traces in monocot cotyledons. The conservative nature of seedling anatomy promises useful evolutionary studies.

Cotyledons with a pair of midveins, as are frequent in gymnosperms like Podocarpus coriaceus, are only occasional in angiosperms (some Austrobaileyaceae, Chloranthaceae, Monimiaceae, and Poaceae). Examples of cotyledons and eophylls exhibiting similar venation patterns are rare.

In the polyclave the term seed leaf is used for the cotyledons after germination.
vernation Vernation (prefoliation) is the disposition of the leaves in the bud. The terminology in existence may be applied also to the relation of the cotyledons to each other in the seed. The types of vernation are:

Conduplicate induplicate: The lamina is folded lengthwise along the veins so that the halves of the upper surface lie together. This type is prevalent in leaves, but rare in cotyledons. The cotyledons of Avicennia are conduplicately folded, one so that its lower surfaces are opposed (reduplicate), the other induplicately embracing it (Duke, 1965a). Monniera, Raphanus, and other genera with orthoplocal embryos are similar to Avicennia.

Conduplicate reduplicate: The lamina is folded lengthwise along the veins so that the halves of the lower surface lie together as in some palm eophylls.

Plicate (pleated): The lamina is folded along the veins, like a closed fan, as in cotyledons of Cordia (Duke, 1965a), and in leaves of Acer.

Convolute: The lamina is rolled lengthwise forming a coil as in the leaves of certain Rosaceae and the cotyledons of many Combretaceae as in Terminalia (Duke, 1965a). According to Lubbock (1891) leaves of Drimys, Kadsura, and Schisandra are convolute. Among Asian mangroves, Rhizophora and Bruguiera have convolute vernation of the leaves, while Carallia, Ceriops, Gynotroches, and Pellacalyx have involute vernation.

Involute: Both margins of the lamina are inrolled lengthwise on the upper surface, as in certain Violaceae and Rhizophoraceae.

Revolute: Both margins of the lamina are inrolled lengthwise on the lower surface, as in many Ericaceae.

Reclinate (inflexed): The upper part of the blade is bent on the lower, as in leaves of Liriodendron. One of the cotyledons of Petiveria in addition to being involute, is doubled back on itself. The second broader cotyledon is convolute or involute about the first. It seems that the scutellum could in many cases represent the end of a reclinate cotyledon.

Circinate: The upper part of the blade is rolled back on the lower, so that the tip is in the center of the coil, as in Cycadaceae and Droseraceae. Certain legume eophylls, e.g., Parkia (Duke, 1965a), approach this type of vernation, while the cotyledons of Cariniana (Fig. 66) have a complex circinate vernation.

Strict: The blade is straight in the bud and expands by growth alone as in many cotyledons and adult leaves.

Vernation of the cotyledons frequently differs from that of eophylls. Major mangrove genera of Panama may be distinguished by virtue of vernation and eophyll arrangement alone. The distinguishing characters are:

Cotyledons strict; leaves involute
Pelliceria
Cotyledons not strict; leaves not involute:
Cotyledons conduplicate . . . . . . . . . . . . . . . . . . . . . . . . . . Avicennia
Cotyledons convolute or conferruminate:
Cotyledons conferruminate; leaves
convolute
Rhizophora Cotyledons convolute; leaves not convolute:

Eophylls opposite Laguncularia
Eophylls alternate . . . . . . . . . . . . . . . . . . . . . . . . Conocarpus
petioles and stipules Sessile and long-petiolate cotyledons may occur on seedlings of the same genus or family, but there is rarely much variability at the specific level. In Bryonia dioica the cotyledons are long-petiolate while in B. laciniosa they are subsessile. Lubbock (1892) speculates that cotyledons tend to be sessile when they are supported by a long hypocotyl, but long-petiolate when borne close to the ground, citing Vitis hypoglauca with short hypocotyls and long cotyledonary petioles and V.cebennensis with long hypocotyl and short petioles. Petioles are often connate at the base as in Lupinus, Podophyllum, and Sanguisorba. On eophylls, the geniculate or incrassate petiole often foreshadows a compound leaf.

Stipules offer good diagnostic characters. Even the cotyledons of certain seedlings, e.g., in Caesalpiniaceae, Fabaceae, Mimosaceae, and Rubiaceae, have obvious stipules. The cotyledons of Prosopis juliflora, in addition to being stipulate, exhibit the nyctinastic tendencies of the foliage leaves. Among some cryptocotylar legumes, e.g., Erythrina spp., (Duke, 1965a), the cataphylls tend to have paired stipules almost equal to those of the eophylls. Stipules of the second eophyll of Acacia farnesiana are spinescent (Duke, 1965a). In stipulate plants, the stipules are usually apparent no later than the second eophyll stage. Stipules are usually apparent on the seedlings but absent from mature branches of species with fugaceous stipules. Stipels are obvious on the first eophylls of some Mimosaceae and Moringaceae, and may be expected in other families whose foliage leaves are characterized by stipels.
indument Presence or absence of indument is not highly definitive, but certain types of indument can be very useful in defining seedlings. Indument provides a main clue for distinguishing three weed-tree species' seedlings in Panama. Eophylls of Cecropia have a white arachnoid indument on the lower surface, while those of Didymopanax have a diffuse, more or less colorless indument. Ochroma eophylls have a close felted grayish indument, rusty at the base of the petioles (Duke, 1965a).

Punctate cotyledons are characteristic of several families (Elaeagnaceae, Malvaceae, Myrtaceae, Primulaceae, Rutaceae). Beneath a tree of Thespesia populnea near Guanica, Puerto Rico, where seedlings similar to those of Ipomoea hispida, as figured by Lubbock (1892). Examination with a lens showed the characteristic pellucid punctation of Thespesia's cotyledons, showing that this was merely an aberrant type with bifid cotyledons such as occur normally in Ipomoea spp. This is apparently the first such aberration reported for the Malvaceae. Montezuma, another malvaceous genus in Puerto Rico, often coexistent with Thespesia, may be distinguished on basis of its stellate hairs.
microscopy When critical determinations are needed, microscopic examination of the seedling will yield further clues. It has been generally agreed that the stomata on various plant parts are of the same type, but Paliwal and Bhandari (1962) point out that "The stomata on the leaves of Michelia and Magnolia are syndetocheilic while those occurring on the outer integument of ovules . . . are of the haplocheilic type." Stomatal types in cotyledons and in adult leaves could also differ; the point deserves investigation. It would be worthwhile to see if distribution of stomata is the same in cotyledons, eophylls, and adult foliage. Hydathodes or glandular mucrons are frequent at the tips of the cotyledons as in Rhus typhina.
eophyll sequence Tomlinson (1960) proposed the term "eophyll" for the first few leaves with green, expanded laminae developed by the seedlings, as opposed to the brown rudimentary scale leaves of fixed number which precede them in most cryptocotylar species. In palms, he noted that the shape and size of the first eophyll is constant and the distribution of its armature and indument is diagnostic. Each palm has its characteristic series of transitional leaves between the eophylls and adult leaves. Similarly characteristic eophyll sequences occur in Anacardiaceae, Bignoniaceae, Caesalpiniaceae, Fabaceae, Meliaceae, Mimosaceae, Sapindaceae, etc., probably in most seedlings whose adults have compound leaves. The eophyll sequence may be abrupt, as in many Mimosaceae with the first eophyll pinnate, the second bipinnate; or delayed, as in many woody Fabaceae, Meliaceae, Sapindaceae, etc., where several cophylls are simple and succeeding ones gradually add leaflets. Often the tumid petiole of an eophyll foreshadows a compound leaf. In some species, there is no sequence, e.g., in Guaiacum, where paripinnate eophylls immediately follow the cotyledons (Duke, 1965a).

There are few reverse sequences in which eophylls are compound and adult leaves simple (Acacia, Ulex). I suspect this would prove to be true of Swartzia sp. (Fig. 22). In Bursera simaruba, the cotyledons are trifoliolate, eophylls simple, and adult leaves compound. In others, the cotyledons are lobate and the eophylls and adult leaves (metaphylls) simple (Tilia). Having cotyledons and eophylls precisely similar, as reported in Dowingia by Lubbock (1892) seems to be quite exceptional. There are few phanerocotylar species with cotyledons broader than the first 12 eophylls (Asclepiadaceae, Cactaceae, Casuarinaceae, Myrtaceae, Proteaceae, e.g.). Several species are known where the eophylls are more conspicuously dentate or lacerate than the adult leaves (Casearia sp., Cordia spp., Ficus, Gustavia (Fig. 65), Quercus, certain members of Quiinaceae, and Rapanea sp.).

Although the eophyll sequence is usually constant, Lubbock (1892) notes a remarkable amount of variation in Ulex europaeus. In some seedlings, the leaves are all simple, in others the primary leaves are simple, subsequent ones trifoliolate; in still others all leaves are trifoliolate. They may be alternate or opposite indiscriminately. All ultimately become modified into simple spines or may be altogether aborted, while the branches form compound or branching spines. Although there are exceptions, the eophyll sequence seems to be characteristic of the species, as do most other characters used to distinguish seedlings. Blastogeny may be added to the other exciting and relatively unexplored fields of investigation, where both variations and constancy may be used in evaluating taxonomic and systematic concepts. Even variability, e.g., heterophylly, as in Morus, Sassafras, and, in Panama, Roupala, seems to be a constant attribute of some taxa.

## Preliminary Systematic Survey ${ }^{1}$

The following descriptions are based on the limited information available, mostly from the author's researches except where otherwise noted. Regrettably, the family description is often based on a single species. To amplify these studies, seeds are requested from any tropical American woody species accompanied by a voucher specimen. Especially desired are representatives of families not included in this paper, then genera, then species. When possible, the seeds will be germinated, illustrated, preserved in the seedling herbarium, with duplicate seedlings returned to the collector who will be duly acknowledged. Herbarium specimens from Latin America are available in exchange for those seeds accompanied by voucher specimens.
podocarpaceat: Germination phanerocotylar, the two cotyledons linear, binervate. Eophylls pseudocotyledonary, like the cotyledons, but uninervate.
gnetaceae: Seeds broadly oblongoid, the outer coat pinkish-red, not striped, the inner coat olive-brown, longitudinally striped. Germination cryptocotylar, with alternate cataphylls (Fig. 1).
arecaceae (palmae): Germination cryptocotylar. Cataphylls alternate. Eophylls simple, bifoliolate, or paripinnate; usually possessing the armature and indument of the adult. Vernation induplicate or reduplicate. The species illustrated (Figs. 2, 3, 4) all have bifoliolate eophylls. Astrocaryum eophylls are already armed and glaucous like the metaphylls (Fig. 4). The specimen illustrated had been grazed by some herbivore.

ARACEAE: Germination cryptocotylar, the cataphylls alternate, linearlanceolate, the first eophyll long-petiolate, hastate, spirally convolute (Montrichar$d i a$, Fig. 5).
smilacaceae: Germination cryptocotylar. Cataphylls alternate; eophylls alternate, with venation like the metaphylls (Fig. 6).

[^1]casuarinaceae: Germination phanerocotylar, the cotyledons narrowly obovate; eophylls verticillate, appressed.

PIPERACEAE: Germination phanerocotylar to subcryptocotylar, monocotylar, anisocotylar, dicotylar, or tricotylar; the cotyledons sometimes retuse. Eophylls usually with aroma, indument, and venation of the metapiylls.
moraceae: Germination cryptocotylar (usually in large-seeded species, Figs. 7 and 8) with alternate cataphylls to phanerocotylar (usually in small-seeded species like Ficus, Fig. 9) without cataphylls, often anisocotylar. Latex, stipules, and indument often characteristic. Eophylls in cryptocotylar species alternate, stipulate, often more conspicuously dentate than the metaphylls, as in Brosimum bernadettae (Fig. 8) [but entire and with caducous stipules in B. utile (Fig. 7)]. Cecropia and Pourouma suggest transitions to Urticaceae.
cannabaceaE: Germination phanerocotylar; the cotyledons sessile, entire, uninerved, or triplinerved. Eophylls near the cotyledons, subsessile, penninerved, with an undulate, rugulose margin, sometimes basally dentate (Fig. 10).
urticaceae: Germination phanerocotylar, often anisocotylar. Cotyledons long-petiolate, often plinerved and reniform. Indument, venation, and arrangement of the eophylls often diagnostic.
olacaceae: Germination cryptocotylar, the stalked cotyledons secund. Hypocotyl glabrous, somewhat swollen. Cataphylls alternate, the upper subtended by spines, grading into alternate, penninerved, glabrous, entire, mucronate eophylls, subtended by spines (Ximenia).
polygonaceae: Germination phanerocotylar, the two cotyledons reniform, subplinerved. Eophylls supracotyledonary, alternate, subconvolute, penninerved, ochreate (Coccoloba). My efforts to germinate Triplaris have failed. Peculiar that a weed-tree should possess such low vitality!
nyctaginaceae: Germination phanerocotylar, at first anisocotylar, the cotyledons becoming subequal, subsessile, reniform, plane, entire, penninerved. Eophylls supracotyledonary, alternate, entire, short-petiolate, penninerved (Neea; Fig. 11).
annonaceae: Germination phanerocotylar, often tardily so, probably cryptocotylar in large-seeded species. Cotyledons lanceolate, subpenninerved. Eophylls alternate, conduplicate. Aroma, indument, and venation often diagnostic.
myristicaceae: Germination cryptocotylar, the secund cotyledons borne in the corrugated seed well above the ground. Eophylls supracotyledonary, alternate, conduplicate, exstipulate, penninerved, entire (Virola, Fig. 12). Latex, indument, and aroma often diagnostic.
monimiaceae: Germination phanerocotylar, the hypocotyl basally swollen, the cotyledons subsessile, broadly ovate, subplinerved and bluntly apiculate in Mollinedia (Fig. 13), uninerved and emarginate in Siparuna (Fig. 14).
lauraceae: Germination cryptocotylar, the epicotyl usually emerging from the cotyledons, i.e., cotyledons not secund. Cataphylls alternate. Eophylls alternate, entire, exstipulate, penninerved. Aroma and indument often diagnostic.


Fig. 1-16. Fig. 1. Gnetum leyboldii $(\times 0.4)$. Fig. 2. Genoma binervia $(\times 0.8)$. Fig. 3. Welfia georgii (Duke 15030; $\times 0.6$ ). Fig. 4. Astrocaryum standleyanum $(\times 0.2)$. Fig. 5. Montrichardia arborescens $(\times 0.4)$. Fig. 6. Smilax sp. (Duke 15077; $\times 0.4$ ). Fig. 7. Brosium utile $(\times 0.2)$. Fig. 8. Brosium bernadetteae $(X 0.4)$. Fig. 9. Ficus insipida (Duke 15195; $\times 0.8$ ). Fig. 10. Cannabis sativa $(\times 0.4)$. Fig. 11. Neea sp. (Duke 15332; $\times 0.4$ ). Fig. 12. Virola sp. $(\times 0.4$ ). Fig. 13. Mollinedia (Duke $15234 ; \times 0.4$ ). Fig. 14. Siparuna (Duke 15128; $\times 0.8$ ). Fig. 15. Capparis pittieri $(\times 0.4)$. Fig. 16. Connarus panamensis ( $\times 0.4$ ).
hernandiaceae: Germination cryptocotylar, the stalked cotyledons secund. Cataphylls alternate, grading into alternate, peltate, subplinerved, entire eophylls (Hernandia).
papaveraceae: Germination phanerocotylar, the cotyledons subsessile, elliptic, entire, plinerved. Eophylls cotyledonary, quercond, with orange latex (Bocconia).
capparaceae: Germination phanerocotylar, the cotyledons plane or slightly planoconvex, subconvolute. Eophylls alternate, entire, penninerved, conduplicate. Capparis pittieri (Fig. 15) has the largest cotyledons of any Capparaceae studied, characteristically raising the gray pubescent testa with them. Several nerves arise at the base of the cotyledon and the hypocotyl is somewhat swollen.
moringaceae: Germination cryptocotylar, the short-stalked cotyledons remaining in the trialate seed. First eophylls supracotyledonary, opposite, decompound, stipellate. As is often true in cryptocotylar species, the plumule is foliate in the ungerminated seed.
chrysobalanaceae: Germination cryptocotylar, the cotyledons secund. Cataphylls alternate, sometimes stipulate, grading into alternate, stipulate, entire, lanceolate to ovate, penninerved eophylls.
connaraceae: Germination cryptocotylar, cataphylls absent. First eophylls supracotyledonary, opposite, often incrassipetiolate, ovate, subcordate, entire. Connarus panamensis (Fig. 16), like Rourea, resembles the seedlings of many Fabaceae, e.g., Ormosia (Fig. 23), and is often dormant at the stage depicted. The absence of stipules on the eophylls separates the Connaraceae from most Fabaceae.
mimosaceae: Germination phanerocotylar to cryptocotylar, with or without cataphylls; eophylls simple to decompound, the sequence gradual to abrupt.

The species of Inga investigated, like I. spectabilis (Fig. 17), have nonphotosynthetic cotyledons, rarely secund, usually auriculate, which are cryptocotylar but escape from the testa shortly after germination. These seeds frequently germinate while still in the pod. Cataphylls are sometimes present, and stipulate. All first eophylls studied are bifoliolate.

Pithecellobium longifolium (Fig. 18) has seedlings comparable to Inga, subcryptocotylar with nonphotosynthetic cotyledons and bifoliolate eophylls. All species of Pithecellobium studied generate the odor of a mercaptan in germinating.

Cotyledons of Pentaclethra (Fig. 19) are somewhat similar, but are green and probably photosynthetic, usually gaping apart at the surface of the soil in the siwamps they frequent, thus not exactly hypogeal nor epigeal, nor cryptocotylar nor phanerocotylar. The first eophylls are decompound.
caesalpiniaceae: Germination phanerocotylar to cryptocotylar, with or without cataphylls, cryptocotylar cataphylliferous germination usually associated with the larger seeds. Probably the most affirmative demonstration of the importance of seedlings to systematics is Léonard's (1957) excellent work on African Caesalpiniaceae, in which he proposes the following hypotheses:


Fig. 17-27. Fig. 17. Inga spectabilis $(\times 0.4)$. Fig. 18. Pithecellobium longifolium (Duke 8212; $\times 0.8$ ). Fig. 19. Pentaclethra macroloba ( $\times 0.1$ ). Fig. 20. Prioria copaifera $(\times 0.1)$. Fig. 21. Mora oleifera $(\times 0.04)$. Fig. 22. Swartzia simplex $(\times 0.4)$. Fig. 23. Ormosia sp. ( $\times 0.4$ ). Fig. 24. Oleiocarpon panamensis ( $\times 0.2$ ). Fig. 25. Maughania sp. (Duke 15448; $\times 0.4$ ). Fig. 26. Myroxylon balsamum $(\times 0.4)$. Fig. 27. Pterocarpus hayesii $(\times 0,4)$.
(a) The establishment of synonymy between genera according to morphological data should be provable by the similarity of their seedlings.
(b) Morphologically related genera, which have the same seedlings, may not be generically distinct.
(c) The partition of a heterogeneous genus into several genera according to their morphological characters, should be provable by the existence of a particular seedling type for each of them.
(d) The existence of several seedling types within one genus may be an indication of a generic heterogeneity that must be checked by other morphological data.
Prioria copaifera (Fig. 20), a swamp forest species, is cryptocotylar with alternate cataphylls succeeded by bifoliolate eophylls which gradually give way to paripinnate metaphylls.

Mora oleifera (Fig. 21), a brackish swamp forest species, with the largest dicot seeds known, is also cryptocotylar with alternate cataphylls succeeded by bifoliolate eophylls succeeded by paripinnate metaphylls.

FAbAcEaE: Germination phanerocotylar to cryptocotylar, with or without cataphylls (in the same genus occasionally). Cataphylls often stipulate. Simple incrassipetiolate eophylls often foreshadow compound metaphylls. Latex, indument, stipules, stipellae, leaf margin, venation, and arrangement often diagnostic.

Cryptocotylar Swartzia (Fig. 22) exhibits the rare reversed eophyll sequence, the imparipinnate eophylls gradually giving way to unifoliolate metaphylls.

Ormosia (Fig. 23) is barely phanerocotylar, the nonphotosynthetic cotyledons often embraced by the nigrescent testa.

Oleiocarpon panamensis (Fig. 24) exhibits an abrupt sequence, the phanerocotylar cotyledons being followed by eophylls similar in structure to the metaphylls.

Maughania, an introduction becoming a regular constituent of the savanna flora, is cryptocotylar, apparently without cataphylls, the eophylls unifoliolate (Fig. 25).

Myroxlon (Fig. 26) is cryptocotylar, without cataphylls, with the first imparipinnate eophylls opposite. This combination of characters shows up in several families with alternate leaves and cryptocotylar seedlings: (1) Species which have cataphylls have the first eophylls alternate while (2) species without cataphylls have the first two eophylls opposite, with subsequent eophylls alternate.

The seedling of Pterocarpus hayesi (Fig. 27) resembles that of P. indica more than that of P. officinalis. It differs from both in having the first eophylls opposite. It is transitional from cryptocotyly to phanerocotyly. Some cotyledons, probably photosynthetic, emerge from the seed but remain secund, others apparently never escape from the seed.
erythroxylaceae: Germination phanerocotylar, the cotyledons oblong, uninerved. Eophylls alternate, supracotyledonary, entire, penninerved, convolute, usually stipulate.
zygophyllaceae: Germination phanerocotylar, the cotyledons subsessile, subtriplinerved, entire, elliptic, glabrous. First eophylls supracotyledonary, opposite, paripinnate (Guaiacum).
rutaceae: Germination cryptocotylar to phanerocotylar, often anisocotylar. Cotyledons and eophylls often aromatic and punctate, a marginal row of glands frequent. Eophyll sequence gradual in compound-leaved species. Polyembryony frequent.

Citrus limonum (Fig. 28) is cryptocotylar, anisocotylar, the cotyledons secund; the eophylls are alternate, punctate, dentate, penninerved, with alate, armed petioles.

Murraya (Fig. 29) is cryptocotylar with alternate cataphylls and dentate, aromatic eophylls.

Simarubaceae: I have not yet observed germination in Quassia (Fig. 30) but suspect it is cryptocotylar. The eophylls suggest certain Mimosaceae, Caesalpiniaceae, and Sapindaceae.
burseraceae: Cotyledons contortuplicate and subcryptocotylar (Dacryodes) to simple and planoconvex (Tetragastris, Protium) or trifoliolate (Bursera) and phanerocotylar. First eophylls simple and opposite (Protium, Tetragastris) or alternate (Bursera, sporadically bifid) to trifoliolate and opposite (Dacryodes). Aroma often diagnostic. Tetragastris panamensis (Fig. 31) is similar to T. balsamifera with auriculate apiculate cotyledons, the eophylls opposite, supracotyledonary, penninerved, entire, or basally auriculate.
meliaceae: Germination cryptocotylar with alternate cataphylls and eophylls (Swietenia) or with no cataphylls and opposite, entire to dentate eophylls (Guarea, Trichilia) to phanerocotylar (Melia, Cedrela).

Carapa (Fig. 32) conforms to the Guarea-Trichilia type.
Cedrela (Fig. 33) has subsessile, entire, plane, narrowly ovoid cotyledons, with alternate, supracotyledonary, trifoliolate, often dentate, eophylls.

Melia (Fig. 34) has petiolate, obovoid, triplinerved, entire cotyledons with the aceroid first eophyll apparently borne at the cotyledonary node.

Trichilia cipo (Fig. 35) differs from other species in that the cotyledons separate but are not strictly opposite or secund.
malpighiaceae: Germination cryptocotylar (especially in alate seeds) without cataphylls to phanerocotylar, often tardy ( 1 year in Byrsonima). Eophylls alternate to opposite, exstipulate, entire, penninerved, the indument often diagnostic.

Although germination in Bunchosia (Fig. 36) is phanerocotylar, the greenishwhite, planoconvex, subsessile cotyledons are probably not photosynthetic. Although I found hundreds of these seedlings beneath a parent tree on San Jose Island and all had aerial cotyledons ("epigeal") I believe that, if the seeds were planted beneath the surface of the soil, the cotyledons would not emerge ("hypogeal"). The eophylls are supracotyledonary, opposite, decussate, entire, penninerved, pubescent.
polygalaceae: Germination cryptocotylar, the subsessile cotyledons secund. Cataphylls alternate, grading into the alternate, entire, narrowly ovate eophylls (Securidaca).
euphorbiaceae: Germination mostly phanerocotylar with long-petiolate cotyledons, subcryptocotylar in Hura and cryptocotylar in Hevea, both, however with long-petiolate, secund cotyledons. Eophyll type, arrangement, indument, venation, glands, and latex often diagnostic.

Hippomane already has poisonous latex at the stage illustrated in Fig. 37. The cotyledons, often cyanotic or bronze-colored, are entire, triplinerved, the petioles with a copious white latex. The first eophylls are supracotyledonary, opposite, dentate, penninerved, subsequent eophylls alternate and stipulate.
anacardiaceae: Germination cryptocotylar (Comocladia) to phanerocotylar with secund [Anacardium excelsum (Fig. 38) and A. occidentale] or opposed cotyledons. Eophylls alternate (Comocladia), opposite (Spondias) or pseudoverticillate (Anacardium, Mangifera). Alternate cataphylls usually present in cryptocotylar species. Eophyll sequence gradual in compound-leaved species.
staphyleaceae: Germination phanerocotylar, the cotyledons subsessile, ovate, entire to retuse, subplinerved. First eophylls supracotyledonary, opposite, trifoliolate, stipulate, and stipellate, the leaflets denticulate. Eophyll sequence gradual (Turpinia).

SApindaceae: Germination cryptocotylar with alternate cataphylls and eophylls (Allophylus, Meliococcus, Sapindus) or without cataphylls and with the first eophylls opposite (Cupania, Maytayba, Paullinia, Serjania, Thouinia); rarely phanerocotylar (Dodonaea).

Talisia nervosa (Fig. 39) suggests Meliococcus, with cryptocotylar germination and alternate cataphylls and bifoliolate alternate eophylls.

SAbiaceae: Germination phanerocotylar, the cotyledons foliar, plane, entire to undulate, subsessile, penninerved. Hypocotyl swollen, glabrous. Eophylls supracotyledonary, alternate, dentate, penninerved (Meliosma, Fig. 40).
rhamnaceae: Germination phanerocotylar, the cotyledons equal, triplinerved, long-petiolate. First eophylls supracotyledonary, opposite, penninerved (Colubrina) or plinerved (Zizyphus), subsequent eophylls alternate.
tiliaceae: Germination phanerocotylar, often associated with the rotting fruit, the cotyledons petiolate, broadly obovate, basally subtruncate, triplinerved, entire (Apeiba aspera, Fig. 41).
malvaceae: Germination phanerocotylar, the cotyledons often convolute, reniform triplinerved to multiplinerved, long-petiolate, often punctate. First eophylls supracotyledonary, alternate, stipulate. Indument and venation often diagnostic.

Hibiscus coclensis (Fig. 42) illustrates the similarity between seedlings of Tiliaceae and Malvaceae.


Fig. 28-40. Fig. 28. Citrus limonum $(\times 0.4)$. Fig. 29. Murraya exotica $(\times 0.6)$. Fig. 30. Quassia amara $(\times 0.4)$. Fig. 31. Tetragastris panamensis $(\times 0.4)$. Fig. 32. Carapa sp. (Duke 14988; $X 0.4$ ). Fig. 33. Cedrela sp. $(\times 0.4)$. Fig. 34. Melia azederach $(\times 0.8)$. Fig. 35. Trichilia cipo $(\times 0.4)$. Fig. 36. Bunchosia cornifolia (Duke 15034; $\times 0.4$ ). Fig. 37. Hippomane mancinella (Duke $11732 ; \times 0.4$ ). Fig. 38. Anacardium excelsum (Duke 8383; $\times 0.3$ ). Fig. 39. Talisia nervosa $(\times 0.4)$. Fig. 40. Meliosma panamensis $(\times 0.4)$.
bombacaceae: Germination cryptocotylar to phanerocotylar, the cotyledons ovate to reniform, subsessile to long-petiolate, subplinerved, the eophylls supracotyledonary, alternate, stipulate, the transition to compound leaves gradual. Hypocotyl often swollen, especially in those species destined to be "bottle trees."

Hampea (Fig. 43) illustrates the convolution of the emerging cotyledons.
Pachira is cryptocotylar with both the cataphylls and eophylls alternate (Fig. 44).

All Quararibea examined are cryptocotylar with alternate cataphylls but with the first pair of eophylls opposite or verticillate (Fig. 45). Dried seedlings have the odor characteristic of the adults.

Matisia cordata (Fig. 46) has rugulose, withered, probably nonphotosynthetic, phanerocotylar cotyledons, with the first eophylls opposite and stipulate.

Sterculiaceae: Germination cryptocotylar to phanerocotylar, often in the same genus (Sterculia, Theobroma). Cotyledons convolute in phanerocotylar, secund in cryptocotylar, species of Sterculia, as e.g., S. costaricense (Fig. 47) and S. apetala.
dilleniaceaE: Germination phanerocotylar, the cotyledons conduplicate, penninerved (Doliocarpus, Fig. 48).
ochnaceae: Germination phanerocotylar (often tricotylar), the cotyledons sessile, enervate, planoconvex, acuminate, often cyanotic, probably not photosynthetic. Eophylls supracotyledonary, alternate but appearing subverticillate, narrowly ovate, exstipulate, penninerved, more conspicuously dentate than the metaphylls (Ouratea, Fig. 49).
marcgraviaceae: Germination phanerocotylar, with little or no hypocotyl, the cotyledons subsessile, uninerved (Fig. 50). Although many seeds germinated, none showed development of the epicotyl. Developmental studies of the family should prove interesting.
pelliceriaceae: Germination subcryptocotylar, the exocarp falling away and exposing the reddish, sessile, planoconvex, nonphotosynthetic cotyledons. Eophylls supracotyledonary, alternate, involute, exstipulate, weakly nerved (Pelliceria, Fig. 51).
clusiaceae: Germination cryptocotylar, the cotyledons secund, cataphylls supracotyledonary, opposite (in all genera studied except Clusia with phanerocotylar, submultiplinerved, equal cotyledons). Latex present in the youngest seedling studied.

Rheedia (Fig. 52) is characteristic of the cryptocotylar species, with opposite, deltoid cataphylls, followed by opposite, entire penninerved eophylls. The illustrated specimen took a year to germinate.
bixaceae: Germination phanerocotylar, the entire, ovate cotyledons weakly triplinerved, punctate-lineate. Eophylls supracotyledonary, alternate, ovate, subcordate, subplinerved, punctate-lineate (Bixa, Fig. 53).


Fig. 41-54. Fig. 41. Apeiba aspera ( $\times 0.8$ ). Fig. 42. Hisbiscus cocleanus (Duke 13934; $\times 0.8)$. Fig. 43. Hampea sp. $(\times 0.4)$. Fig. 44. Pachira aquatica $(\times 0.1)$. Fig. 45. Quararibea asterolepis (Bristan 1335; $\times 0.4$ ). Fig. 46. Matisia cordata ( $\times 0.2$ ). Fig. 47. Sterculia costaricana ( $\times 0.3$ ). Fig. 48. Doliocarpus sp. $(\times 0.4)$. Fig. 49. Ouratea lucens (Duke 8298; $\times 0.4)$. Fig. 50. Marcgraviaceae $(\times 3.2)$. Fig. 51. Pelliceria rhizophorae $(\times 0.4)$. Fig. 52. Rheedia sp. (Duke 11980; $X 0.4$ ). Fig. 53. Bixa orellana ( $X 0.6$ ). Fig. 54. Cochlospermum vitifolium $(\times 0.4)$.

Cochlospermaceae: Germination (after 1 year) phanerocotoylar, the cotyledons short-petiolate, linear-lanceolate, entire, uninerved. Eophylls supracotyledonary, alternate, aceroid. Latex orange (Cochlospermum, Fig. 54).
violaceae: Germination phanerocotylar, the cotyledons subsessile, entire, triplinerved, the eophylls supracotyledonary, alternate, penninerved, coarsely dentate [more so than metaphylls, stipulate (Duke No. 15005)]; or germination cryptocotylar, the cotyledons sessile, not secund, with subopposite cataphylls grading into subopposite eophylls (Gloeospermum, Fig. 55).
flacourtiaceae: Germination phanerocotylar, the cophylls supracotyledonary, alternate, stipulate, penninerved, often pellucid-punctate or lineate, usually more conspicuously dentate than the metaphylls.

Mayna (Fig. 56) is a typical flacourtiaceous seedling.
passifloraceae: Germination phanerocotylar, the cotyledons long-petiolate, elliptic, entire, plinerved, the eophylls supracotyledonary (Fig. 57), alternate, variable in shape and venation; less commonly cryptocotylar (Fig. 58).
cactaceae: Germination phanerocotylar, anisocotylar, the cotyledons subsessile, plane, broadly ellipsoid, entire, penninerved, ultimately becoming almost equal, with axillary spines; eophylls supracotyledonary, subopposite, tardily spinescent, rather like the cotyledons (Pereskia, Fig. 59).

The anisocotylar, planoconvex, linear cotyledons of Wittia (Fig. 60) are the only leaves on this epiphyte.
lecythidaceae: Apparently there are two germination types in Panama's Couratari (Fig. 61 and Fig. 62). Correa and Dressler No. 793 is phanerocotylar, the hypocotyl slightly tetragonal, the cotyledons ovate, rugulose but plane, penninerved. In C. panamensis, however, the cotyledons remain in the winged seed, followed by supracotyledonary eophylls, suggestive of the cotyledons in the phanerocotylar species. Cataphylls are absent.

The seedlings of Eschweilera (Fig. 63) and Lecythis (Fig. 64) conform to the Gustavia type (Fig. 65), cryptocotylar with alternate cataphylls and eophylls.

Gustavia superba (Fig. 65) is cryptocotylar, the epicotyl arising between the corrugated, planoconvex cotyledons, with alternate cataphylls, grading into alternate, exstipulate, lanceolate to oblanceolate eophylls, proportionately more dentate than the metaphylls.

Cariniana pyriformis (Fig. 66) has very distinctive phanerocotylar germination, the aceroid lobate cotyledons subcircinately embraced in the testa which is raised with the cotyledons. The drip-tips of the cotyledons are very conspicuous as they unfold. The eophylls are supracotyledonary, alternate, penninerved, and more conspicuously dentate than the metaphylls.
rhizophoraceae: Germination cryptocotylar, without cataphylls, the eophylls supracotyledonary, opposite, exstipulate, penninerved, entire, glabrous (Rhizophora).


Fig. 55-68. Fig. 55. Gloespermum sp. (Duke 15268; $\times 0.4$ ). Fig. 56. Mayna sp. (Duke 14963; $\times 0.4$ ). Fig. 57. Passiflora sp. (Duke $13270 ; \times 0.4$ ). Fig. 58. Passiflora sp. (Duke 15287; $\times 0.4$ ). Fig. 59. Pereskia bleo $(\mathrm{A} \times 1.2 ; \mathrm{B} \& \mathrm{C} \times 0.4)$. Fig. 60 . Wittia sp. $(\times 0.4)$. Fig. 61. Couratari panamensis $(X 0.4)$. Fig. 62. Couratari sp. (Correa \& Dressler 793; $X 0.4$ ). Fig. 63. Eschweilera (Bristan 22; $X 0.4$ ). Fig. 64. Lecythis sp. (Blume s.n. "monkey pot"; $\times 0.4$ ). Fig. 65. Gustavia superba ( $X 0.1$ ). Fig. 66. Cariniana pyriformis $(X$ 0.4). Fig. 67. Syzygium sp. (Duke 15302; $X 0.8$ ). Fig. 68. Eugenia malaccense ( $\times 0.4$ ).
combretaceae: Germination phanerocotylar, the cotyledons reniform, convolute, the eophylls supracotyledonary, alternate or opposite, exstipulate.
myrtaceae: Seedlings, like the embryos, diagnostic for certain generic groups, cryptocotylar and often polyembryonic in those characterized by conferruminate planoconvex cotyledons (Eugenia, Fig. 68; Syzygium, Fig. 67) (cataphylls present or absent); phanerocotylar with broadly ovate subsessile cotyledons (Gomidesia, Myrcia), or with lanceolate, uninerved cotyledons (Psidium). Punctations, indument, and aroma are often diagnostic.
melastomaceae: Commonly the germination is phanerocotylar, the eophylls decussate with the cotyledons.

Mouriri parvifolia (Fig. 69), however, is cryptocotylar, the cotyledons secund in the testa, which is raised above the soil. Supracotyledonary, opposite cataphylls and eophylls are mostly borne in the same plane.
araliaceae: Germination phanerocotylar, the cotyledons broadly ovate, plinerved to penninerved, the eophylls simple, often telescoped at the cotyledonary node; the eophyll sequence gradual.
myrinaceae: Germination phanerocotylar, sometimes operculate, the cotyledons equal or anisocotylar, the margins entire or undulate, often punctate or lineate and cyanotic; eophylls usually supracotyledonary, alternate, conduplicate exstipulate (Ardisia spp., Figs. 70 and 71).

SAPOTACEAE: Germination cryptocotylar, without cataphylls but with secund cotyledons, to phanerocotylar, the cotyledons dark green and coriaceous. Eophylls usually supracotyledonary and alternate. Latex usually obvious at an early stage.
oleaceat: Germination phanerocotylar, the cotyledons subsessile; eophylls supracotyledonary, opposite.
apocynaceae: Germination usually phanerocotylar, the cotyledons ovate, cordate to auriculate, triplinerved. Eophylls supracotyledonary, alternate, lanceolate to oblanceolate, entire, penninerved. Latex copious (Plumeria).

Lacmellea edulis (Fig. 72) is cryptocotylar, the stalked cotyledons secund; cataphylls opposite, eophylls lanceolate, opposite, weakly nerved. Latex copious, sticky, white.

Stemmadenia (Fig. 73) has phanerocotylar, ovate, entire to undulate, glabrous, penninerved, subsessile cotyledons with copious latex, the eophylls supracotyledonary, entire, penninerved, decussate with the cotyledons.
asclepiadaceae: Germination phanerocotylar, the elliptic cotyledons long-petiolate, penninerved, with white latex. First eophylls supracotyledonary, opposite (Calotropis).
cordiaceae: Germination phanerocotylar, the cotyledons deltoid, subsessile to long-petiolate, plicate, undulate to crenulate. Eophylls supracotyledonary, alternate, penninerved, usually more prominently dentate than the metaphylls. Cystoliths and indument often diagnostic.


Fig. 69-82. Mouriri parvifolia $(\times 0.4)$. Fig. 70. Ardisia sp. (Duke 14989; $\times 0.4$ ). Fig. 71. Ardisia sp. (Duke 15132; $\times 0.4$ ). Fig. 72. Lacmellea edulis $(\times 0.4)$. Fig. 73. Stemmadenia sp. (Duke 13161; $\times 0.4$ ). Fig. 74. Enallagma latifolia $(\times 0.4)$. Fig. 75. Crescentia cujete (Blume 3656; $\times 0.4$ ). Fig. 76. Coussarea cerrojefensis ( $\times 0.4$ ). Fig. 77. Pentagonia sp. $(\times 0.4)$. Fig. 78. Cephaelis correae (Duke 15010; $\times 0.8$ ). Fig. 79. Tocoyena pittieri $(\times 0.4)$. Fig. 80. Alibertia edulis (Blume 3734; $X 0.6$ ). Fig. 81. Borojoa sp. (Bristan 140; $\times 0.4$ ). Fig. 82. Faramea occidentalis $(\times 0.4)$.
verbenaceae: Germination phanerocotylar, the cotyledons ovate, entire, subtriplinerved, short-petioled. Eophylls supracotyledonary, opposite, decussate with the cotyledons, often more dentate than the metaphylls. Indument often diagnostic, e.g., the punctate glands in Tectona impart a red-spotted outline of the seedling to the newspaper in which it is pressed.
avicenniaceae: Germination phanerocotylar, one cotyledon conduplicate about the other, slightly unequal, broadly reniform, subcordate, sometimes emarginate. Eophylls supracotyledonary, opposite, decussate with the cotyledons, entire, lanceolate to ovate, weakly penninerved.
solanaceae: Germination phanerocotylar, the cotyledons ovoid, penninerved, entire, long-petiolate. Eophylls supracotyledonary, alternate, exstipulate (Cestrum).
bignoniaceae: Germination usually phanerocotylar, the cotyledons narrowly to broadly reniform, enervate to plinerved, deeply emarginate to bilobate, cordate to auriculate. Eophylls supracotyledonary, usually opposite and decussate with the cotyledons, simple (in species with simple or digitate metaphylls, e.g., Crescentia, Fig. 75), dentate (in species with pinnate metaphylls) or compound (in species with decompound metaphylls).

Enallagma (Fig. 74) is the only cryptocotylar species studied. Note the opposed cataphylls which follow the retuse cotyledons. Although the cotyledons may escape from the testa as it putrifies, they are brownish-black and nonphotosynthetic.
rubiaceae: Germination usually phanerocotylar, the cotyledons narrowly to broadly ovoid, subplinerved, entire, subsessile to long-petiolate, usually stipulate. Eophylls supracotyledonary, opposite, decussate with the cotyledons, stipulate.

Tocoyena pittieri (Fig. 79) illustrates a fairly common deviation in which the testa (and/or endosperm) is raised characteristically with the cotyledons (cf. also Fig. 76 and 77) which tardily escape to become phanerocotylar. This state is but a step away from true cryptocotyly, as in Faramea occidentalis (Fig. 82).

## Bibliography

Bailey, I. W. 1956. Nodal anatomy and vasculature of seedlings. Jour. Arnold Arb. 37: 269-287.
Boyd, L. 1932. Monocotylous seedlings: Morphological studies in the postseminal development of the embryo. Trans. Proc. Bot. Soc. Edinburgh 31: 5-224.
Carlquist, S. 1961. Comparative plant anatomy. Holt, Rinehart \& Winsion, New York. 146 pp.
Compton, R. H. 1912. An investigation of the seedling structure in the Leguminosae. Jour. Linn. Soc. London, Botany 41: 1-122.
Corner, E. J. H. 1954. The durian theory extended. II. The arillate fruit and the compound leaf. Phytomorph. 4: 152-165.
Cronquist, A. 1968. The evolution and classification of flowering plants. Houghton Mif flin Co., Boston. 396 pp.
Davis, G. L. 1966. Systematic embryology of the angiosperms. John Wiley \& Sons, New York. 528 pp.
Duke, J. A. 1964a. Prelude to the polyclave. I. Embryo. Roneo, Durham, North Carolina. $30 \mathrm{pp} .+$ iv.
-——. 1964b. Prelude II: Seed. Roneo, Durham, North Carolina. 19 pr. in eight forest types in Puerto Rico. Ann. Missouri Bot. Gard. 52: 314-350.
————. 1965b. Prelude III: Sterile specimens. Roneo, Durham, North Carolina. 39 pp. 1965c. Prelude IV: Flower. Roneo, Durham, North Carolina. 28 pp.
———. 1965d. Prelude to a palm polyclave. Roneo, Durham, North Carolina. 14 pp . olina. 8 pp . -- . 1969. Legume polyclave. 288 characier cards for legume genera. 36 pp. Xerox transparency. Columbus, Ohio. Jan. 13.

1969b. Family polyclave. 770 character cards for spermatophyte families. Battelle Memorial Institute, 77 pp.
___-_ (in press). Woody seedlings. In: H. T. Odum (ed.), Radiation Ecology and a Rain Forest.
---., C. R. Gunn, and E. E. Terrell (unpublished). Prelude to a grass polyclave. 330 character cards for grass genera.
Eames, A. J. 1961. Morphology of the Angiosperms. McGraw-Hill Book Co., Inc., New York. 518 pp.
Earle, F. R. and Q. Jones, 1962. Analyses of seed samples from 113 plant families. Econ. Bot. 16: 221-250.
Fernald, M. L. 1950. Gray's manual of botany. 8th cd. American Book Co., New York. 1632 pp.
Leonard, J. 1957. Genera des Cynometreae et des Amherstieae africaines (Leguminosae Caesalpinioideae); Essai de blastogénie appliquée à la systématique. Academie royale de Belgique, Classe des sciences, Memoires, Collection in-8, $30(1677)$, Fas. 2: 1-314, 23 phoios.
Lubbock, J. 1891. On stipules, their form and function. Pt. I. Jour. Linn. Soc. London, Botany 28: 217-243.
————. 1892. A Contribution to Our Knowledge of Secdlings. 2 vols. London. 608, 646 pp .
Marrero, J. 1949. Tree seed data from Puerto Rico. Caribbean Forester 10: 11-26.
Martin, A. C. 1946. The comparative internal morphology of seeds. Amer. Midland Nat. 36: 513-660.
Melville, R. 1962. A new theory of the angiosperm flower I. Kew Bull. 16: 1-50.
Murley, M. R. 1951. Seeds of the Cruciferae of northeastern North America. Amer. Midland Nat. 46: 1-81.
Paliwal, G. S. and N. M. Bhandari. 1962. Stomatal development in some Magnoliaceae. Phytomorph. 12: 409-412.
Reeder, J. R. 1957. The embryo in grass systematics. Amer. Jour. Bot. 44: 756-768.
Sporne, K. R. 1954. A note on nuclear endosperm as a primitive character among dicotyledons. Phytomorph. 4: 275-278.
Stebbins, G. L. and G. S. Khush. 1961. Variations in the organization of the stomatal complex in the leaf epidermis of monocotyledons and its bearing on their phylogeny. Amer. Jour. Bot. 48: 51-59.
Swamy, B. G. L. and P. M. Ganapathy. 1957. On endosperm in dicotyledons. Bot. Gaz. 119: 47-50.
Tombinson, P. B. 1960. Seedling leaves in palms and their morphological significance. Jour. Arnold Arb. 41: 414-428.


[^0]:    ${ }^{1}$ Studies supported in part by the U.S. Atomic Energy Commission, Nevada Operations Office, Contract No. AT (26-1)-171.

[^1]:    ${ }^{1}$ Presented at the Second Symposium on Amazonian Biota in Florencia, Colombia, January 23, 1969, and submitted for publication in Spanish in the proceedings of the symposium.

